Jaffe, K. 1984.

J. theor. Biol. (1984) **106,** 587–604

[21 February 1984]

Negentropy and the Evolution of Chemical Recruitment in Ants (Hymenoptera: Formicidae)

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(*Received* 3 *March* 1983, *and in final form* 19 *September* 1983)

The applicability of the concept of negentropy to the study of evolution is tested by tracing the phylogeny of the information content of the communication systems used for recruitment in the Formicidae. Data from the literature is reviewed and ordered around theoretical evolutionary routes based on increasing negentropy of the chemical communication systems used. One pathway presupposes the development of chemical orientation prior to chemical attraction, i.e. signalling the presence of food; whereas the others begin with the chemical attraction of nestmates without orientation with chemical cues to the food. The results suggest that the Myrmicinae, Ponerinae, Dolichoderinae, Pseudomyrmycinae and possibly Dorylinae evolved chemical recruitment via chemical attraction, whereas the Formicinae evolved chemical recruitment via chemical orientation. These alternative patterns permit the establishment of phyletic trends based on glandular evolution for chemical recruitment. The results are compared with phylogenetic studies based on morphological and chemical characters, and it emerges that the recruitment behaviour proves to be a particularly conservative characteristic, in that it is evident in the same form in a wider range of species. The conclusion is reached that the negentropy content of living systems is a powerful tool in phylogenetic studies, even of small taxonomic groups.

Introduction

The use of behavioural characters in phylogenetic studies has proved highly productive (Lorenz, 1971). Tracing primitive behavioural traits is difficult because there may be no living species showing the trait and behavioural fossils do not exist. Criteria to define the evolutionary degree of behaviour are therefore necessary. Negentropy is proposed here as are such criteria. Different authors had suggested that the phenomenon of live and of evolution of living systems is related to the concept of increase in the order of the system; where order is considered to be negative entropy (Schrödinger, 1944; Waddington, 1964; Weiss, 1970; Eigen, 1971; Monod, 1971; Lorenz, 1973; Rechenberg, 1973; Weizsäcker, 1974; Riedel, 1976). The increase

0022–5193/84/040587+18 $03.00/0 © 1984 Academic Press Inc. (London) Ltd.

in negentropy though is believed to be evident in broad evolutionary terms only. The aim of this work is to evaluate the validity of this criteria in small taxonomic groups.

The communication system used in recruitment to food in ants has been extensively studied (Wilson, 1971; Law & Regnier, 1971; Hölldobler, 1978; Dumpert, 1978; Hölldobler & Engel, 1978; Parry & Morgan, 1979), and the information is thus available to test the application of negentropy to evolution. The negentropy concept used here corresponds to the formulation $-\Delta S = \Delta I = k \log (p_0/p)$, where p_0/p indicates the reduction of available choices out of a maximum p_0 possible, due to the existing information I.

Recruitment in Ants

Of the different communication systems used by ants for recruitment, whether to food, to new nests or for defence, "chemical mass recruitment" (Wilson, 1971) seems to be the more efficient and sophisticated (Jaffe, 1980). In chemical mass recruitment, the foraging ant recruits a huge number of nestmates using only trail pheromones, which are secreted on the ground and attract and guide nestmates to the food source.

A theoretical analysis of the communication system involved in chemical mass recruitment (Jaffe, 1980) indicates important aspects. This recruitment system seems to be the most efficient available to ants which forage at localized food sources. Chemical signals alone suffice to produce mass recruitment. Maximum efficiency in recruitment is achieved by separating the spatial information from information about the quality of the food find. This may be achieved by using two pheromones, or different threshold levels of the same pheromone.

Other communication systems for recruitment described for ants are as follows

Tandem running (Hingston, 1929), occurs when the foraging ant attracts a nestmate using antennal contact and then leads it "in tandem" to the food source. The recruited ant follows closely behind the "scout", frequently contacting the abdomen of the leader with its antennae. No chemical signals are used.

Tandem running with odour signals (Dumpert, 1978), occurs when the scout ant uses chemical cues for either orienting itself back to the food source, or to help attract nestmates, as in *Camponotus sericeus* (Hölldobler 1974*a*) and in *Leptothorax* species (Möglich, 1979). This last system is also called "tandem calling".

Group recruitment occurs when the scout ant recruits a group of up to thirty nestmates at a time, as in *Camponotus pennsylvanicus* (Traniello,

1977). Chemical signals are used but other signals, such as antennal contacts, etc., are important.

Chemical mass recruitment (Wilson, 1971) is considered to be the most developed recruitment technique. Scout ants guide hundreds or thousands of nestmates to the food source by chemical means only.

Great intra-generic variations in these recruitment techniques make it difficult to establish phyletic trends in the Formicidae (Bruyn, 1977). Hölldobler (1978) and Dumpert (1978) proposed that in the Formicinae, the evolutionary sequence was from "tandem running" through group recruitment to chemical mass recruitment; whereas in the Myrmicinae, the route was from "tandem calling" through group recruitment to chemical mass recruitment. No detailed phyletic relations based on these definitions are possible.

The Theoretical Evolutionary Routes

It is proposed that any optimal communication system for recruitment to food must acomplish the following functions. Orientation (o): orientation of ants from the nest to the food source; attraction (a): signalling the presence of food, attracting to the food; regulation of the attraction (a'): giving information about the quality and/or quantity of the food source, where the concept quality may be related to the accessibility of the food in addition to the nutritive value of it (Taylor, 1978).

Some of these functions may be acomplished by one signal, which informs of the presence of the food and of the quality of the food at the same time. However, a signal which informs about the quality of the food, but not of the presence of food is not logically possible, although the reverse situation is possible. As regards orientation, we may theoretically concieve a signal which orientates the ants to the food and gives information about its presence at the same time, but separate signals for each of these functions are also possible solutions. We thus postulate three evolutionary routes which are theoretically plausible, following the trends of increasing negentropy:

$$o \rightarrow o+a \rightarrow o+a+a';$$

$$a \rightarrow a+o \rightarrow o+a+a';$$

$$a \rightarrow a+a' \rightarrow o+a+a'$$

The remaining possibilities:

$$o \rightarrow o+a' \rightarrow o+a+a';$$

$$a' \rightarrow a'+o \rightarrow o+a+a';$$

$$a' \rightarrow a'+a \rightarrow o+a+a';$$

may be excluded on the reasons given above. In Fig. 1, the plausible routes and their combinations are represented graphically. Here, the amount of negentropy is thought to be equivalent to the amount of information a system is able to transmit, the possible information being *a*, *a'* and *o*.

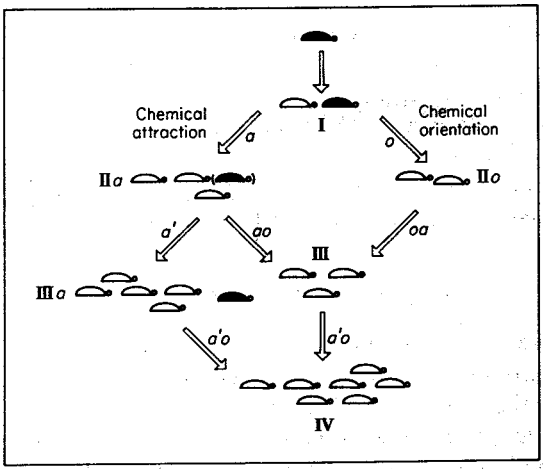

FIG. 1. The evolution of "pure chemical recruitment" (stage IV) through different theoretical stages. *o*, *a* and *a'*, symbolize the evolution of chemicals used for orientation of ants to the food; signalling of the presence of food, i.e. attraction; and for modulated attraction respectively. Ants are schematically symbolized with open figures, whereas scout ants are represented with dark figures.

The information *o*, *a*, *a'* may be transmitted by visual, mechanical, or chemical signals singly or in combination. In order to simplify the model and the search in the literature, only chemical signals are taken into account in this exercise. Chemical signals seem to be more efficient than visual or mechanical signals in ant societies, since evolution substitutes other kinds of signals with chemical signals (Hölldobler, 1978; Jaffe, 1980, 1984).

We may then postulate that pure chemical recruitment evolved through at least two different main routes (Fig. 1), each one departing from stages of low negentropy such as "tandem running" with tactile stimuli only, or individual foraging systems in which no information is transfered from one individual to another (stage I, Fig. 1). The next level of sophistication (stage II) would be either first develop mechanisms to orient individuals chemically towards the goal (by a trail), or to secrete an attracting chemical at the food site, as a trail, or at the nest entrance. Attractive chemicals will increase the probability of an ant finding the food, without necessarily orientating them from the nest to the food, by increasing exploratory behaviour for example. After the development of chemical orientation mechanisms

mechanical and/or visual attraction by a scout ant could be replaced by the evolution of a chemical message that would bring ants to the site or to the trail (stage III). Quantitative information, i.e. information about the quality and quantity of the food could be transcribed through the chemical(s) responsible for attraction and thus make possible a precisely regulated recruitment (stage IV). Thus, optimum chemical recruitment is reached via steps II*o*–III–IV (Fig. 1).

The pathway beginning with the evolution of chemical attraction signals (steps II*a* onwards, Fig. 1), offers two choices. Natural selection might either sophisticate the existing chemical attraction system, providing it quantitative information and then develop compounds for chemical orientation (steps II*a*–III*a*–IV); or chemical orientation could evolve first, and then the chemical attraction system could aquire quantative meaning (steps II*a*–III–IV, Fig. 1).

In all the different evolutive steps, scout ants are necessary. Scout ants using chemical orientation signals do not have to be present during all phases of recruitment, whereas scouts attracting their nestmates chemically may also exert guiding functions during some phases of recruitment. Therefore, where no chemical orientation exists, a scout ant is represented in Fig. 1.

The characteristics of each of these evolutionary stages would be as follows.

I. *Non-chemical recruitment*, such as tandem running. Scout ants recruit one or more nestmates to the food find, using mechanical and/or visual signals only; or individual foraging systems.

II*o*. *Chemical orientation without chemical attraction* (*o*). A chemical trail from the food source to the nest helps scouts and/or nestmates to orientate to the food, and/or back home. Attraction with mechanical and/or visual signals may exist.

II*a*. *Chemical attraction without chemical orientation* (*a*). Scout ants attract nestmates partially or totally by chemical means, sometimes guiding them to the food find using mainly mechanical and/or visual signals, as in "tandem calling" for example. Another possibility is that the recruiting ant induces its nestmates to forage, without guiding them to the food, but increasing the possibilities of finding the food, as in some *Pseudomyrmex* species (Jaffe, 1984).

III. *Chemical orientation with chemical attraction* ($o+a$). Scouts lay trails which attract workers and orientate them to the food. Mechanical and/or visual signals may improve recruitment. No regulation of the amount of recruitment through chemical signals is possible, but visual or mechanical messages can be used for this purpose.

III*a*. *Regulated chemical attraction without chemical orientation* ($a+a'$). Scout ants attracts nestmates by chemical means only, and regulate the number of ants recruited through secretion of different concentration of the attractant. Guiding to the food is necessary because the attractant has to be short-lived (Jaffe, 1980). However, guiding may be done from a short distance, being equivalent to short-range orientation. Thus, continuously reinforced trails of the attractant could serve as chemical orientation signals. These trails are not stable and it is expected that such trails will change position continuously.

IV. *Pure chemical recruitment* ($o+a+a'$). Chemicals serve as orientation signals and as attractants, and the concentration of the chemical regulates the amount of recruitment produced. Pure chemical recruitment is equivalent to "chemical mass recruitment" (Wilson, 1971; Jaffe, 1980).

From Fig. 1 it is clear that steps II*a* and III*a* are excluded from the evolutionary route via chemical orientation, whereas step II*o* is excluded

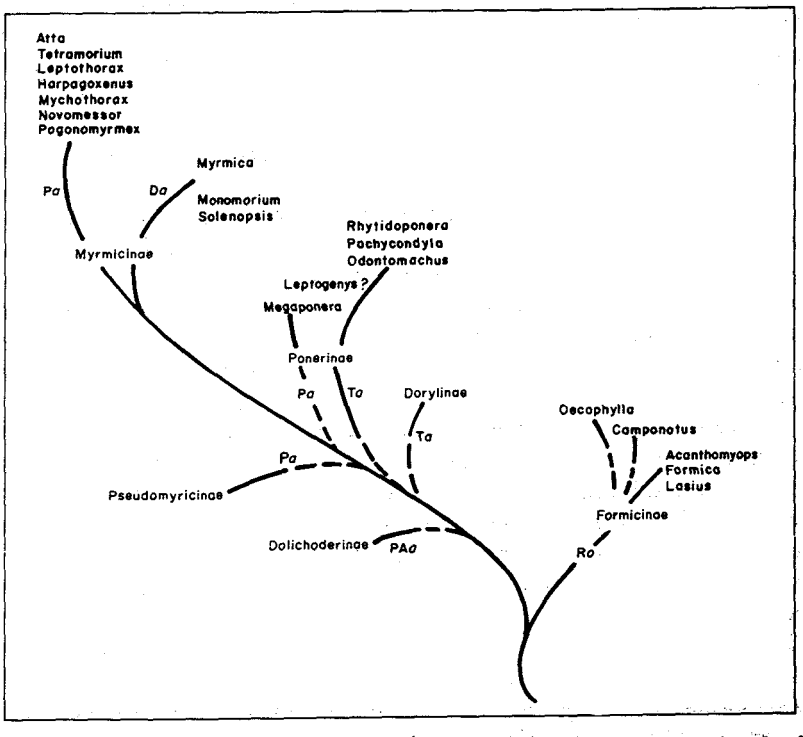

FIG. 2. Phyletic trends in formicid chemical recruitment system. The abbreviations for the glands and its function are the same as in Table 1.

from the route via chemical attraction. All other steps may be reached by either of the routes. Thus, species with recruitment systems corresponding to steps II*o*, II*a* and III*a* are specially helpful in tracing the evolution of recruitment in ants.

In order to fit the available data from the literature (Table 1, at the end of the text) to the postulated theoretical steps, the following assumptions were made: regulation of recruitment itself is no indication as to the degree of evolution of chemical recruitment, because regulation may be achieved by mechanical or visual signals, for example by "waggle dances" (Möglich, Maschuitz & Hölldobler, 1974). A chemical attractant for recruitment is a pheromone which induces workers to forage or explore if presented at the nest entrance, or which attracts workers to it if presented as a trail or as a dot. An attractive chemical is active only for a few minutes (Jaffe, 1980). Chemical orientation is supposed to exist when a trail pheromone has orientating effects on workers, even hours after the substance has been deposited on the trail. The presence of chemical signals for recruitment is taken to indicate more recently evolved communication systems.

If we now fit the ant species whose recruitment systems are known (Table 1) to the different evolutionary stages described, we obtain the dendrogram in Fig. 2. Here, the glandular source of the recruitment pheromone(s) is also taken into account, and Brown's (1954) nomenclature of the subfamilies and grouping of genera into subfamilies is maintained.

Discussion

In each subfamily of ants only one of the two main theoretical pathways proposed in Fig. 1 shows up (Table 1). In the Formicinae only stages of the route II*o*–III–IV are found; whereas in the Myrmicinae, Pseudomyrmicinae, Ponerinae and Dolichoderinae only steps of routes II*a*–III*a*–IV or II*a*–III–IV are observed. This fact suggests the function of the first chemical signal evolved by that corresponding group of ants, i.e. chemical orientation or attraction. If we suppose that the chemical signal is produced by an exocrine gland and, if we further suppose irreversibility in evolution (at least a very low probability), we exclude the possibility of a reversion in the function of the chemical signals produced by a gland. Therefore we are able to tell which of the different glands used for recruitment by a given subfamily was the first one to be associated with recruitment in the evolutionary history of the group. In applying these criteria to the data in Table 1, we find that the first gland to evolve chemical signals for recruitment in the Formicinae is the rectal sac, whereas in the Dolichoderinae, Ponerinae, Pseudomyrmicinae and Myrimicinae, the first gland produced an attractant. A phylogenetic scheme based on these criteria is represented in Fig. 2.

These findings (Fig. 2) are in agreement with the phyletic trends based on the morphology of the sting apparatus (Blum & Hermann, 1978). Both propose a separation of the Formicinae from all other subfamilies. These relations partly contradict the propositions of Robertson Dudzinski & Orton (1980), who emphasizes an evolutionary tie between the Ponerinae, Dorylinae and Formicinae because they all produce trail pheromones in the rectal sac, and they suggest a phyletic relationship between the Myrmicinae and Dolichoderinae since they use trail pheromones produced by glands of the female reproductive system. Brown (1954) and Taylor (1978) proposed a common origin for the Formicinae and the Dolichoderinae based on external morphological characters, which partly contradicts the results represented in Fig. 2.

These data imply that the tergal gland produced the first recruitment pheromone in *Odontomachus, Leptogenys, Pachycondyla, Rytidoponera* (Ponerinae) and *Neivamyrmex* and *Eciton* (Dorylinae); the genus *Megaponera* (Ponerinae) seems to be the exception, since it appeared to have evolved chemical recruitment through use of the poison gland as did most of the Myrmicinae. In the Myrmicinae, two main groups are apparent: in one, chemical recruitment is achieved by starting to use the poison gland; in the second, the Dufour's gland is employed first. Genera using the poison gland as a source for attractional signals in recruitment include *Mychothorax, Harpagoxenus, Leptothorax, Tetramorium, Novomessor, Pogonomyrmex* and the Attini. The second generic group which uses the Dufour's gland to secrete the attractant consists of the genera *Myrmica, Monomorium* and *Solenopsis* (Fig. 2). From this pattern it is possible to postulate that the first generic group of the Myrmicinae is more related to the Ponerinae *Megaponera* than the second group. Except for some minor contradictions regarding the placement of the genera *Myrmica* and *Pogonomyrmex*, the phylogenetic pattern described for the Myrmicinae agrees well with Kugler's (1979) findings based on the morphology of the sting apparatus. The Formicinae all share the character of using the rectal sac as the source of an orienting trail pheromone.

Finer subdivisions could be established for the Myrmicinae and perhaps for other subfamilies if the evolutionary routes II*a*–III–IV and II*a*–III*a*–IV (Fig. 1) are taken into account. In the Myrmicinae, the group using the Dufour's gland for chemical attraction appears to have used the route over step III, whereas both routes seem to have been used by myrmicines using the poison gland for chemical attraction (Table 1). More data is required before finer analysis is attempted.

The Dorylinae have several special features. Their nomadic predatory habits have undoubtedly influenced the evolution of their recruitment system. From the data available it is not clear which route they have followed

in evolution. It may be similar to the one of the Ponerinae (Hölldobler & Engel, 1978). Perhaps their system is derived from a more advanced one (step IV, Fig. 1), and fulfills their special requirements of communicating new nest sites and new food sources at the same time.

Another interesting feature is the utilization of a second gland for recruitment. The suggestion of Robertson *et al.* (1980), that the Dolichoderinae use the poison gland in addition to the Pavan's gland for chemical orientation, should be investigated. Data on the secondary glands used for recruitment is also meager in the Ponerinae and Myrmicinae. Thus far only *Leptogenys chinensis* (Ponerinae, Table 1) has been reported to use two secretions, the poison gland for orientation and the tergal gland for attraction. In the Myrmicinae, documentation exists for *Myrmica rubra*, *Monomorium pharaonis* and *Pogonomyrmex badius* (Table 1). *Atta cephalotes* utilize one gland to perform both, orientation and attraction. Certainly other ants also use two glands for recruitment. In the case of *Crematogaster* and *Melissotarsus*, this study would predict a gland secreting an attractant, possibly part of the female reproductive system.

It can be reasonably assumed that recruitment system II*o* is more efficient for the exploitation of fixed food resources than system II*a*. System II*a* on the other hand should be more appropriate for the exploitation of scattered food, like small arthropods for example. This would imply that the Formicinae were the first that extensively exploited fixed food resources, as they were the only group to evolve chemical recruitment through system II*o*. The most probable fixed resources are sugar secretions of aggregates of homopterans, which could explain the highly specialized symbiosis between many Formicinae and Homoptera (Way, 1963). The other groups probably specialized in predating arthropods and thus, even today, their association with homopterans is rather opportunistic (Wilson, 1971; Way, 1963).

The examination of the function of hitherto neglected glands, such as the valves gland (Bazire-Benazet & Zylberberg, 1979), sternal and tergal glands (Hölldobler & Engel, 1978), and the use of alarm pheromones in short range recruitment such as the one reported for *Megaponera foetens* (Longhurst, Baker & Howse, 1979) or *Oecophylla longinoda* (Hölldobler & Wilson, 1978) and *Pogonomyrmex badius* (Wilson, 1971), could provide further information for the study of evolution of chemical recruitment in ants.

Conclusions

In spite of great differences in levels of negentropy found, even between species of the same genus, it was possible to trace phyletic relations in the Formicidae. This exercise, based only on the negentropy of the chemical

communication system used during recruitment to food, showed three routes that equally maximized negentropy. The phyletic relations based on these routes are surprisingly similar to those phyletic trees build on several morphological, physiological and behavioural characters (Blum & Hermann, 1978; Taylor, 1978; Kugler, 1979; Hölldobler, 1978) although they contradict some of the more earlier studies (Brown, 1954; Eisner, 1957; Roberston, 1968; Hermann, 1969). The advantage of the method used in this work is that it allows for an eventual quantitative analysis. There is no doubt that a final conclusion about the phylogeny of this group requires a synthesis of all the different types of characters.

It could be confirmed that some behavioural characters change very slowly in formicid phylogeny, contrary to the common belief that the behavioural repertoire of a species represents recent adaptations to the environment. If the rate of evolutionary change in the recruitment systems is compared, for example, with the rate of evolutionary change in the biosynthesis of pheromones (Howse & Bradshaw, 1980), it can be seen that different species vary enormously in the chemicals produced, whereas the recruitment systems show slow changes, being the same through various subfamiles in some cases.

The assumption that the evolution of living systems follows the trend of decreasing the amount of entropy of the system has never been systematically checked before in small taxonomic units. The fact that even at the subfamily level, these criteria seem to be valid, would indicate that the negentropy concept is applicable at all levels of evolution of biological systems. In any case it would be interesting to find out where it does not apply.

I am in debt to Dr Michael D. Robinson for his helpful discussions and for critically reading the manuscript. This study was partially supported by grant S1-1336 of CONICIT, Venezuela.

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TABLE 1.

Summary of ant recruitment systems and the glands used in chemical communication.

	Recruitment System		Reference
Myrmeciinae	1		Wilson (1971)
Myrmecia gluosa	1 (*T*)		Robertson (1971), Kugler (1978)
Pseudomyrmecinae			
Pseudomyrmex pallidus	*P*		Blum & Callahan (1963)
Pseudomyrmex termitarius	1 *a*	II*a*	Jaffe & Lopez (unpublished)
Pseudomyrmex triplarinus	1	I	Jaffe & Aragot (unpublished)
Dorylinae			
Aenictus eugenii	2	I	Gottwald & Cunningham (1976)
Neivamyrmex nigrescens°	3 R*o*T*a*(III*a*)	IV	Schneirla (1971), Wilson (1971), Watkins (1964), Topoff & Mirenda (1975, 1978), Topoff & Lawson (1979), Topoff *et al.* (1980)
Eciton hamatum°	4 R*o*T*a*	IV	Blum & Portocarrero (1966), Chadab & Rettenmeyer (1975), Hölldobler & Engel (1978)
Dolichoderinae			
Iridomyrmex pruinosum	PA		Wilson & Pavan (1959)
Iridomyrmex humilis°	PA*a*(P)(*o*)(R)	III*a*(IV)	Wilson & Pavan (1959), Robertson *et al.* (1980), Van Vorhis *et al.* (1981), Cavill *et al.* (1976)
Tapinoma sessile	PA		Wilson & Pavan (1959)
Tapinoma nigerium	PA		Couret & Passera (1979)
Tapinoma erraticum	PA		Couret & Passera (1979)
Tapinoma israelis	3	(II*a*)	Szlep & Jacobi (1967)
Tapinoma simothi	3	(II*a*)	Szlep & Jacobi (1967)
Azteca sp.	4 *a*	III*a*	Jaffe & Alvarez (unpublished)
Monacis bispinosa	PA		Wilson & Pavan (1959)
Conomyrma sp.	4 *a*	III*a*	Jaffe & Colmenares (unpublished)
Ponerinae			
Paraponera clavata	1	I	Yung & Hermann (1980)
Ponera eduardy	2	I	Le Masne (1952)

Bothroponera soror	2	I	Longhurst (1977)
Pachycondyla laevigata	2 T		Hölldobler & Traniello (Hölldobler & Engel, 1978)
	R		Blum (1966)
Bothroponera tesserinoda°	2 *a*	II*a*	Hölldobler *et al.* (1973), Maschwitz *et al.* (1974)
Pachycondyla harpax	2 T		Hölldobler & Engel (1978)
Pachycondyla crassa	2 T*a*	II*a*	Hölldobler & Engel (1978)
Rhytidoponera metallica	T*a*		Hölldobler & Haskins (1977)
Paltotyreus tarsatus	S		Hölldobler & Engel (1978, Sudd (1962)
Leptogenys attenuata	1 (P)		Fletcher (1971)
Leptogenys nitida	3 P		Fletcher (1971)
Leptogenys diminuta	3 P		Maschwitz & Muhlenberg (1975)
Leptogenys ocellifera	4 P*a*(*o*)	IV(III*a*)	Maschwitz & Muhlenberg (1975)
Leptogenys chinensis	4 P*o* T*a*	IV	Maschwitz & Muhlenberg (1975), Maschwitz & Schohegge (1977)
Odontomachus bauri	1	I	Jaffe & Marcuse (1984)
Odontomachus haematoda	2 (T)*a*	II*a*	Hölldobler & Engel (1978)
Megaponera foetens	3 P(*oa*)	III	Levieux (1966), Longhurst *et al.* (1979*a*), Longhurst & Howse (1979)
Ectatomma ruidum	1 (*a*)	I–II*a*	Jaffe & Marquez (unpublished)
Formicinae			
Cataglyphis bicolor	1	*I*	Harkness & Wehner (1977)
Formica subintegra	R		Regnier & Wilson (1971)
Formica rufa	R*o*		Hangartner (1967)
Formica cinera	R*o*		Hangartner (1967)
Formica lugubris	3		Hangartner (1967)
Formica fusca°	3 R*o*	II*o*	Möglich & Hölldobler (1975)
Formica polyctena	4 R*o*	III	Horstmann (1976)
Lasius niger	1 (R*o*)	(II*o*)	Hangartner (1967)
Lasius emarginatus	R*o*		Hangartner (1967)
Lasius flavus	R*o*		Hangartner (1967)
Lasius fuliginosus	4 R*o*	III	Hangartner (1967), Carthy (1951)
Acanthomyops interjectus°	4 R*oa*	IV	Hangartner (1970)
Oecophylla longinoda°	3 R*oSa*	III	Hölldobler & Wilson (1978)
Camponotus sericeus°	2 R*o*	II*o*	Hölldobler (1974*a*), Hölldobler *et al.* (1974), Möglich (1973)
Camponotus paria	2 R*o*(*a*)	II*o*	Hingston (1929)

TABLE 1—(*contd.*)

	Recruitment System		Reference
Camponotus compressus	2 R*o*(*a*)	II*o*	Hingston (1929)
Camponotus beebei	R*o*		Wilson (1959*a*)
Camponotus rufipes	R*o*(*a*)	II*o*–III	Sanchez & Jaffe (unpublished)
Camponotus pennsylvanicus:	3 R*o*P*a*	III	Traniello (1977), Hartwick *et al.* (1977)
Camponotus socius°	3 R*o*P*a*	III	Hölldobler (1971*a*)
Myrmelachista ramulorum	R		Blum & Wilson (1964)
Paratrechina longicornis	R		Blum & Wilson (1964)
Myrmicinae			
Crematogaster sumicrasti	4 TA*a*(*o*)	IV(III*a*)	Jaffe & Pino (unpublished)
Crematogaster ashmeadi	TA*o*(*a*)	III	Leuthold (1968)
Crematograster pergingueyi	4 TA	IV	Fletcher & Brand (1968)
Melissotarsus titubans	TA		Delage-Darchen (1972)
Cardicondyla venustura	2	I	Wilson (1959*a*)
Cardicondyla emeryi	2	I	Wilson (1959*a*)
Chelaner antarcticum	1	I	Blum (1966)
Pristomyrmex pungens	4 P		Hayashi & Komae (1977)
Mychothorax spp.	2 P*a*	II*a*	Möglich (1979)
Harpagoxenus spp.	2 P*a*	II*a*	Möglich (1979)
Harpagoxenus sublaevis	2 Pa	II*a*	Möglich (1979), Buschinger & Winter (1977)
Harpagoxenus americanus	2 *ao*	(III)	Möglich (1979), Wesson (1939)
Leptothorax muscorum	2 P*a*	II*a*	Möglich (1979), Möglich *et al.* (1974)
Leptothorax nylanderi	2 P*a*	II*a*	Möglich (1979), Möglich *et al.* (1974)
Leptothorax acervorum°	2 P*a*	II*a*	Möglich (1979), Möglich *et al.* (1974), Dobrizanski (1966)
Leptothorax duloticus	3 P*a*	(III*a*)	Möglich (1979), Alloway (1979)
Decamorium uelense	3 P(*a*)		Longhurst *et al.* (1979*b*)
Tetramorium guineense	3 P(*a*)		Blum & Ross (1965)
Tetramorium caespitum	3 P(*a*)		Blum & Ross (1965)
Myrmica fracticornis	P		Cammaerts (1974), Blum (1974)
Myrmica emeryana	P		Cammaerts (1974), Blum (1974)
Myrmica americana	P		Cammaerts (1974), Cammaerts *et al.* (1977)
Myrmica scabrinodis	4 P*o*D*a*	III-IV	Cammaerts *et al.* (1978), Cammaerts & Cammaerts (1980)

Myrmica sabuleti	4 P*o*D*a*	III-IV	Cammaerts & Cammaerts (1980)
Myrmica ruginodis	3 P*o*D*a*	III	Cammaerts & Cammaerts (1980)
Myrmica rugulosa	3 P*o*D*a*	III	Cammaerts & Cammaerts (1981)
Myrmica rubra°	3 P*o* D*a*	III	Cammaerts *et al.* (1976, 1977), Abraham & Pasteels (1980)
Monomorium antarcticum	1	I	Blum (1966)
Monomorium floricola	P		Blum (1966)
Monomorium minimum	P		Blum (1966)
Monomorium subopacum	3	(II*a*-III)	Szlep & Jacobi (1967)
Monomorium venustum	3	(II*a*-III)	Szlep & Jacobi (1967)
Monomorium pharaonis°	3 P*o* D*a*	III	Blum (1966), Hölldobler (1973)
Huberia striata	P		Blum (1966)
Manica bradleyi	P		Blum (1974)
Manica hunteri	P		Blum (1974)
Manica mutila	P		Blum (1974)
Novomessor albisetosus	3 P*a*	III*a*	Hölldobler *et al.* (1976), Markl & Hölldobler (1978)
Novomessor cockerelli°	3 P*a*	III*a*	Hölldobler *et al.* (1978), Markl & Hölldobler (1978)
Pogonomyrmex californicus	P (D)		Hölldobler & Wilson (1970)
Pogonomyrmex rugosus	3 P*a* (D*o*)		Whitford (1979), Regnier *et al.* (1973)
Pogonomyrmex barbatus	4 P*a* (D*o*)	IV	Hölldobler (1974*b*, 1976, 1979)
Pogonomyrmex maricopa	4 P*a*	III*a*	Hölldobler (1974*b*, 1976, 1979)
Pogonomyrmex badius°	4 P*a* D*o*	IV	Hölldobler & Wilson (1970), Hölldobler (1971*b*)
Veromessor pergandei	4 P		Blum (1974)
Solenopsis saevissima	4 D*oa*	(IV)	Wilson (1959*b*, 1962)
Solenopsis invicta	4 D*oa*	(IV)	Barlin *et al.* (1976)
Solenopsis richteri	4 D*oa*	(IV)	Barlin *et al.* (1976)
Solenopsis xylomi	4 D*oa*	(IV)	Barlin *et al.* (1976), Taylor (1977), Wilson (1962)
Solenopsis occidentalis	4	(IV)	Taylor (1977)
Solenopsis geminata	4 D*oa*	III*a*(IV)	Barlin *et al.* (1976), Taylor (1977), Wilson (1962), Hangartner (1969) Puche & Jaffe (unpublished)
Pheidole pallidulata	3 *oa*	III	Szlep (1970)
Pheidole teneriffana	3 *oa*	III	Szlep (1970)
Phidole fallax	4 D		Law *et al.* (1965)
Pheidole dentata	4 P		Wilson (1967*a*)
Daceton armigerum	1	I	Blum & Portocarrero (1966)
Zacryptocerus varians	4 (PD)*a*	II*a*-III*a*	Wilson (1979*b*)
Cyphomyrmex rimosus	P		Blum *et al.* (1964)

TABLE 1—(*contd.*)

	Recruitment System		Reference
Trachymyrmex septentrionalis	P		Blum *et al.* (1964), Robinson *et al.* (1974)
Trachymirmex urichi	P*ao*	III	Villegas & Jaffe (unpublished)
Acromyrmex landolti	4 P*ao*	IV	Navarro & Jaffe (unpublished)
Acromyrmex versicolor	4 P	IV	Blum *et al.* (1964)
Acromyrmex octospinosus°	4 P*oa*	IV	Blum *et al.* (1964), Jaffe & Howse (1979)
Atta cephalotes°	4 P*oa*	IV	Blum *et al.* (1964), Jaffe & Howse (1979)
Atta sexdens	4 P	IV	Moser & Blum (1963), Riley *et al.* (1974), Cross *et al.* (1979)
Atta texana	4 P	IV	Riley *et al.* (1974), Moser & Blum (1963), Blum *et al.* (1964) Tumlinson *et al.* (1971)

1 = individual foraging, 2 = tandem running, 3 = group recruitment, 4 = chemical mass recruitment; *R* = rectal sac, *P* = poison gland, *D* = Dufour's gland, *S* = sternal gland, *T* = tergal or pygidial gland, *PA* = Pavan's gland, *TA* = tarsal glands. The suffixes *o* and *a* after the abbreviation of the gland indicates if the pheromone secreted by this gland is used for orientation (long trailing effect) or as attractant (short-lived effect). I, II*o*, etc. correspond to evolutionary stages in Fig. 1 and in the text. Parenthesis indicate contradictory or insufficient data.